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Intraspecific facilitation explains the persistence of *Phragmites australis* in modified coastal wetlands

VALÉRIE C. REIJERS,^{1,†} MARLOES VAN DEN AKKER,¹ PETER M. J. M. CRUIJSSEN,¹
LEON P. M. LAMERS,¹ AND TJSSE VAN DER HEIDE^{1,2,3}

¹Department of Aquatic Ecology & Environmental Biology, Faculty of Science, Institute for Water and Wetland Research, Radboud University, Nijmegen 6525 AJ The Netherlands

²Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen 9700 CC The Netherlands

³Department Coastal Systems, Royal Netherlands Institute for Sea Research and Utrecht University, Den Burg 1790 AB The Netherlands

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Abstract. Coastal exploitation and human-mediated modifications have markedly altered the community composition and functioning of coastal wetlands worldwide. Although recent work has shown that harnessing positive density-dependent feedbacks can greatly enhance the recovery of habitat-modifying species in degraded wetlands, the role of these intraspecific feedbacks in explaining the persistence of altered, unfavorable plant communities remains largely unexplored. Here, we experimentally tested whether intraspecific facilitation may explain the persistence of common reed (*Phragmites australis*) in human-modified coastal wetlands. We performed a full-factorial mesocosm experiment crossing low-density pioneer versus high-density established development stages with saline (20 psu) versus freshwater conditions. Results showed a clear shift in plant growth response from intraspecific competition under freshwater conditions to self-facilitation in saline treatments. We identified two positive feedback mechanisms enabling the established treatment to overcome salinity stress: (1) Enhanced root oxygenation of the sediment at higher plant density decreased accumulation and intrusion of phytotoxic sulfide, and (2) density-dependent rainwater infiltration into the soil lowered salinity in the dense root mat, preventing salt stress. Our study demonstrates that intraspecific facilitation can be an important factor in explaining the persistence of *Phragmites australis* in coastal wetlands. We emphasize the importance of integrating positive interactions in coastal restoration but argue that they should either be harnessed when restoring vegetation or broken when eradication of nontarget species is the management objective.

Key words: coastal wetlands; habitat modification; osmoregulation; *Phragmites australis*; restoration; self-reinforcing feedbacks; sulfide toxicity.

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† **E-mail:** v.reijers@science.ru.nl

INTRODUCTION

Coastal wetlands provide numerous vital ecosystem services, including coastal flood protection, carbon storage, water purification, and the provision of staging, nesting, or nursery habitat for waterbirds and fish species (Beck et al. 2001, Zedler and Kercher 2005, Ma et al. 2010,

Barbier et al. 2011, Hopkinson et al. 2012, Costanza et al. 2014). However, these valuable ecosystems have degraded extensively over the last centuries and are still declining at alarming rates—with over 60% lost in the last century—primarily as a result of human activities such as wetland exploitation and conversion to agricultural land (Bertness et al. 2002, Lotze et al. 2006,

Gedan et al. 2009, Silliman et al. 2012, Davidson 2014, Sheaves et al. 2014, Dixon et al. 2016). For example, human manipulation of natural hydrodynamic processes, through the construction of dikes or dams, has altered plant community composition by reducing the influence of seawater and preventing the storm-mediated transport of organic material (Gedan et al. 2009). Shifts in habitat-modifying (i.e., ecosystem engineering) species abundance can have far-reaching ecological and economic effects when they affect natural ecosystem processes such as surface accretion, carbon storage, or food web structure (Kirwan and Megonigal 2013, Osland et al. 2014, Park et al. 2017).

Although it is now increasingly acknowledged that the loss of natural coastal wetlands should be reversed, restoration of degraded wetlands has been proven to be notoriously difficult. Despite the \$1,040,000 (2010 USD) per hectare investment, ~40% of restoration attempts do not result in successful rehabilitation of target species (Bayraktarov et al. 2016). An important underlying reason for this low investment–success ratio is the tight coupling between habitat-forming species and their physical environment, in which a higher density of habitat modifiers improves environmental conditions accordingly (i.e., intraspecific facilitation; Suding et al. 2004, Silliman et al. 2015). In degraded and barren wetlands, the harsh environmental conditions—for example, high soil salinity/sulfide levels and wave exposure—inhibit vegetation re-establishment and restoration is rarely successful (Howes et al. 1986, Bouma et al. 2009). Recent work has shown that restoration success in unvegetated wetlands can be significantly increased by adopting planting designs that are aimed at maximizing positive interactions—by clumping plants in dense aggregations—rather than spacing them out to minimize potential negative interactions (Silliman et al. 2015). However, to what extent intraspecific facilitation increases the persistence of nontarget plant communities in human-modified wetlands remains largely unexplored. Yet, if the nontarget plant community can increase its environmental tolerance range by modifying its physical environment, restoration of the original abiotic conditions by, for example, removing dikes or lowering nutrient loading may not suffice to restore the pre-disturbance ecosystem community and functions.

Here, we examined whether intraspecific facilitation may be key factor in explaining the persistence of native common reed, *Phragmites australis* (Cav.) Trin. Ex Steud., (hereafter *Phragmites*) in modified coastal wetlands (see Appendix S1: Fig. S1 for a graphical representation of our hypothesis). *Phragmites* is known as a successful invader in marine coastal zones and inland salt marshes, causing extensive ecological and economic damage (Zedler et al. 1990, Chambers et al. 1999, Lynch and Saltonstall 2002, Altartouri et al. 2014, Hazelton et al. 2014). Although the well-known invasion of North American coastal marshes is primarily caused by the introduction of an aggressive Eurasian genotype (Saltonstall 2002), native strains in both the United States and Europe are also expanding their ecological range and are increasingly intruding and attaining dominance in more saline environments (Lynch and Saltonstall 2002, Altartouri et al. 2014). This habitat expansion has been attributed to increasing anthropogenic disturbances in coastal areas, leading to changes in hydrodynamic processes (e.g., construction of dams or drainage ditches), increased nutrient loading, and decreased grazing pressure, that facilitate the establishment of the species (van Deursen and Drost 1990, Menard et al. 2002, Silliman and Bertness 2004, Bart 2006, King et al. 2007). Once established, however, *Phragmites* has proven to be particularly difficult to remove and restoring the abiotic conditions (e.g., tidal regime and nutrient loading) alone may be insufficient to rehabilitate the original halophytic communities (Konisky and Burdick 2004, Válega et al. 2008, Hazelton et al. 2014). Thus far, this persistence has been ascribed to increased physiological tolerance of the Eurasian invasive haplotype (Saltonstall 2002, Vasquez et al. 2005) and mediation of environmental stress through clonal integration, (Amsberry et al. 2000, Bart and Hartman 2000, Chambers et al. 2003). However, another potential, yet untested, explanation could be that *Phragmites* relies on density-dependent modifications of the edaphic conditions to mitigate physiological stress in saline environments. Although natural establishment of *Phragmites* in saline conditions is very difficult, low-salinity windows in disturbed coastal wetlands can promote initial colonization after which intraspecific facilitation may cause established *Phragmites* stands to

persist after the pre-disturbed hydrodynamic conditions are restored.

To test our hypothesis, we manipulated native European common reed (*Phragmites australis*) stands to reflect both established (clonally integrated) and pioneer (unconnected rhizomal fragments) stands and assigned them to freshwater and saline conditions in a full-factorial design. We used the relative growth and survival rates as proxies to determine the success of both types of *Phragmites* stands in overcoming the physiological stress saline environments provide. In addition, we collected detailed information on both soil conditions and plant physiology to identify possible feedback mechanisms.

MATERIALS AND METHODS

Site description

The experiment was conducted using plant material from a mesohaline (11.1 ± 0.1 psu at time of collection; Appendix S1: Fig. S2) *Phragmites* marsh on the Wadden Sea island of Schiermonnikoog, The Netherlands ($53^{\circ}29'51''\text{N}$, $6^{\circ}13'10.6''\text{E}$). The coastal *Phragmites* marsh is situated on a former beach plain behind a man-made sand-drift dike, which has altered the inundation regime of the back-barrier marsh since 1959. The reduced influence of seawater intrusion and the increased potential for freshwater seepage in the area led initially to the establishment of species-rich mosaics of halophyte and calciphyte plant communities (van Tooren et al. 1993). However, over time, the isolated setting of the modified back-barrier marsh prevented the transport of organic matter out of the system and favored the establishment of more late-successional species such as *Phragmites*. The first sightings of *Phragmites* in this area date back to 1982, and since then, it has rapidly taken over the marsh replacing former biodiverse communities (see Appendix S1: Fig. S3 for the observed *Phragmites* distributions over time; van Tooren et al. 1993, Pranger and Tolman 2012). Due to the presence of the artificial sand barrier, which obstructs seawater flow from the North Sea, seawater now only intrudes the marsh during spring-tide-related storm surges, when the water table is raised beyond 2.80 m above mean water level (MWL). The relative low position of the area—combined with a threshold at 2.80 m MWL at

the entrance of the marsh—prevents seawater from flowing out of the system, and saline conditions can prevail for several months. Depending on the rainfall and evaporation rates, this can result in strongly fluctuating salinity levels in the upper soil layers (Olf et al. 1993, Reijers et al. 2019a, b; Appendix S1: Fig. S2).

Plant material

Intact winter-dormant (i.e., no live above-ground biomass) common reed (*Phragmites australis*) sods were cut in March 2015 from the back-barrier marsh of Schiermonnikoog and transported in 53 plastic containers (l:w:h = $50 \times 45 \times 30$ cm) to the greenhouse facility of the Radboud University. The sods were cut in close proximity from each other (total area removed was $\sim 24 \text{ m}^2$) to minimize genetic differences between the experimental units. The dormant culms that had died off after the previous growing season were cut at ~ 5 cm above the ground to standardize starting conditions, while ensuring that they remained above water level. The pioneer treatment was created by first carefully removing the entire rhizomal network from a randomly selected subset of half of the experimental units, after which five healthy rhizomal fragments (12.28 ± 2.12 g FW; 21.02 ± 1.94 cm length) were replanted in the original soil of each manipulated unit. Although the soil of the pioneer treatments was inevitably disturbed during the removal of the rhizomal network, the soil of the established treatments was likewise disturbed when we manually removed all bulbs, roots, and rhizomes of other species (e.g., *Bolboschoenus maritimus*, *Agrostis stolonifera*, and *Potentilla anserina*). Both the established and pioneer treatments were flushed repeatedly with rainwater and kept at freshwater (1.2 ± 0.1 psu) conditions during a 10-week acclimation period.

Experimental setup

The potential importance of intraspecific facilitation in mitigating the negative effects of saline conditions was tested by crossing the two *Phragmites* treatments (pioneer vs. established) with both saline and freshwater conditions in a 2×2 factorial design. This full-factorial design yielded four treatment combinations: pioneer saline (PS), pioneer freshwater (PF), established saline (ES), and established freshwater (EF), with 13 (PS; PF;

EF) to 14 replicates (ES) per treatment (see Appendix S1: Fig. S4 for pictures taken at the end of the experiment). For the saline treatment, artificial diluted seawater (20 psu) was made by dissolving synthetic sea salt (Tropic Marin Sea salt, Tropic Marin, Hünenberg, Switzerland) in deionized water. At the start of the experiment, the salinity levels as measured in the porewater were 19.4 ± 3.5 psu for the pioneer saline treatment and 20.3 ± 2.7 psu for the established saline treatment with no significant difference between the two ($t_{22} = 0.78$; $P = 0.45$). The freshwater treatments were kept at the initial salinity levels obtained during the acclimation period, which resulted in near-freshwater conditions with 1.00 ± 0.24 psu for the pioneer treatment and 0.48 ± 0.10 psu for the established treatment. Moreover, at the end of the acclimation period the length of the plants was 17.6 ± 1.0 cm for the low-density pioneer treatment and 19.7 ± 1.1 cm for the high-density established treatment with no significant differences between the two ($t_{50} = 1.36$; $P = 0.18$). The experiment lasted for 39 d and was conducted at an open greenhouse facility of the Radboud University, where the experimental units were placed randomly to control for potential differences in temperature and light. The open greenhouse facility—which has a roof but no walls—allows for near-ambient conditions except for the direct influence of rain. Watering was done manually using deionized water to keep the plants under constant waterlogged conditions at ~1 cm above soil surface. During the experiment, all sods were weeded once or twice a week to maintain monocultures of *Phragmites*.

Plant analyses

To calculate their growth rates (cm/d), the lengths of all individual shoots in the pioneer treatment were measured at the start and at the end of the experiment. For the established treatments, ten randomly selected shoots were marked and measured at the start of the experiment and remeasured at the end. At the end of the experiment, shoots with more than 20% living tissue were classified as being alive, while the others were considered deceased.

After the final harvest, aboveground tissue from the measured shoots was pooled into a single subsample (1.90 ± 0.44 g FW) per experimental unit,

which was then freeze-dried, ground using a ball mill (M301; Retsch, Haan, Germany), and stored for further analyses. Subsequently, C and N concentrations were determined using an elemental analyzer (Carlo Erba NA1500; Thermo Fisher Scientific, Waltham, Massachusetts, USA), and stable sulfur isotope ratios between ^{34}S and ^{32}S ($\delta^{34}\text{S}$) were analyzed using dynamic flash combustion ratio mass spectroscopy (Thermo Scientific Delta V Advantage plus EA 1110; Thermo Fisher Scientific) with BaSO_4 as a standard. Furthermore, concentrations of sulfur (S), sodium (Na), phosphorus (P), and iron (Fe) were determined on 100 mg of the aboveground plant material through digestion with 4 mL of HNO_3 (65%) and 1 mL of H_2O_2 (30%) in a microwave oven (MLS 1200 Mega; Milestone, Sorisole, Italy), after which the samples were diluted and analyzed using an inductively coupled plasma emission (ICP) spectrophotometer (ICP-OES iCAP 6000; Thermo Fisher Scientific). Free proline concentration (a proxy for osmotic stress) of the aboveground shoots was determined by extraction using norvaline as internal standard on 50 mg freeze-dried material according to van Dijk and Roelofs (1988). The freeze-dried extracts were dissolved in 0.01 N HCl and analyzed by high-performance liquid chromatography (Varian 920-LC Analytical HPLC; Varian, Palo Alto, California, USA).

Biogeochemical analyses

Sediment porewater samples were anaerobically collected at the end of the experiment using 60-mL vacuumed syringes connected to 10-cm Rhizon samplers (Eijkelkamp, Giesbeek, The Netherlands). Total sulfide concentrations in the porewater were measured immediately after sampling in a mixture of 50% sulfide anti-oxidation-buffer and 50% sample, using an ion-specific silver-sulfide electrode (Lamers et al. 1998). In addition, concentrations of phosphate (PO_4^{3-}), nitrate (NO_3^-), and ammonium (NH_4^+) were measured colorimetrically on an AutoAnalyzer 3 system (Bran & Luebbe, Norderstedt, Germany, or Skalar and Seal AutoAnalyzer), using ammonium molybdate-, sulfanilamide-, and salicylate-based methods, respectively (Lamers et al. 1998). After diluting (three times) and acidifying the sample using 1% nitric acid (HNO_3), the concentration of iron (Fe) was measured using ICP spectrometry (Appendix S1: Fig. S5).

Statistical analyses

All statistical analyses were performed using the software program R (version 3.3.2, R Development Core Team 2017). The interactive effects of the saline conditions and *Phragmites* treatment on both survival and growth of the shoots were analyzed using generalized linear mixed models (GLMMs, lme4 package in R) with a binary logistic and a Gaussian distribution, respectively, and with experimental unit as a random factor. For fitting GLMMs, we first started by testing the complete model with all treatments and interactions and stepwise reduced the model by excluding nonsignificant interactions. As the complete statistical models with all treatments and interactions showed significant effects and interaction for both response variables (i.e., growth and survival), no further model reduction was required. Two-way factorial ANOVAs were conducted to assess the main and interactive effects of saline conditions and *Phragmites* treatment on different biogeochemical and plant physiological parameters. For every test, normality of the residuals was checked and, if needed, the data were transformed using a square root or Box–Cox transformation. *P*-values lower than 0.05 were considered statistically significant.

RESULTS

Plant growth response

At the end of the experiment, all shoots in the freshwater treatments were alive. The growth rate differed between the *Phragmites* treatments with the plants in the pioneer treatment having a higher growth rate than the plants in the established treatment (Fig. 1). In contrast, saline conditions negatively impacted both the survival and growth of *Phragmites*, but this effect was much smaller in the established treatment compared to the pioneer treatment (Fig. 1). In the salinity treatment, shoot survival in the pioneer treatment was reduced to 62%, whereas survival in the established units remained very high at 97% ($\chi^2(1, N = 1016) = 157,796$; $P < 0.001$; Fig. 1a). The growth rates of the shoots were on average 80% lower in saline conditions compared to the freshwater conditions (0.68 cm/d [F] vs. 0.15 cm/d [S]; $\chi^2(1, N = 468) = 446$; $P < 0.001$; Fig. 1b). However, we found a strong interaction between the type of *Phragmites* stand (pioneer vs.

established) and the conditions in which the plants were grown ($\chi^2(1, N = 468) = 64$; $P < 0.001$). Within the saline conditions, we found plants in the established treatment to grow twice as fast as the plants from the pioneer treatment (0.19 cm/d [ES] vs. 0.10 cm/d [PS]). In the freshwater treatment, a reversed effect was found: Plants in the pioneer treatment grew on average 48% faster than the plants in the established treatment (0.82 cm/d [PF] vs. 0.55 cm/d [EF]).

Soil and plant physiochemical response

The addition of diluted seawater led to increased salinity, and enhanced dissolved sulfide levels (Fig. 2a, d). However, we found both stressors to be significantly lower in the established treatment compared to the pioneer. Porewater salinity in the pioneer treatment increased over the course of the experiment from 19.4 ± 0.9 to 22.7 ± 0.9 psu, whereas the salinity of the established treatment decreased from 20.3 ± 0.7 to 17.0 ± 0.4 psu ($F_{1,49} = 7.08$; $P = 0.010$; Fig. 2a). Proline concentrations in the shoots were strongly enhanced in the salinity treatment ($21.4 \mu\text{mol/g}$ [S] vs. $1.51 \mu\text{mol/g}$ [F]; $F_{1,49} = 361.14$; $P < 0.001$; Fig. 2b). In addition, we found an interaction of type of *Phragmites* stand with the salinity treatment, with two times higher proline concentrations in the pioneer saline treatment ($29.7 \mu\text{mol/g}$ [PS] vs. $13.1 \mu\text{mol/g}$ [ES]; $F_{1,47} = 7.09$; $P = 0.045$). The same was observed for the Na:K ratio, with an on average fifteen times higher ratio in the leaves of the plants grown under saline conditions (0.89 [S] vs. 0.06 [F]; $F_{1,48} = 364.14$; $P < 0.001$; Fig. 2c). Similar to proline, a strong interaction effect of type of *Phragmites* stand with salinity resulted in a strong increase of Na concentrations in the leaves in the pioneer treatment ($1.32 \mu\text{mol/g}$ [PS] vs. $0.47 \mu\text{mol/g}$ [ES]; $F_{1,48} = 26.19$; $P < 0.001$).

Porewater sulfide concentrations in the salinity treatments were, on average, more than twice as high in the pioneer versus the established units ($802 \mu\text{mol/L}$ [PS] vs. $315 \mu\text{mol/L}$ [ES]; $F_{1,49} = 7.34$; $P = 0.009$; Fig. 2d). The lower sulfide concentrations in the established units were accompanied with a 55% decrease of total sulfur concentrations in the leaves ($141.3 \mu\text{mol/g}$ [ES] vs. $219.2 \mu\text{mol/g}$ [PS]; $F_{1,48} = 12$; $P = 0.001$; Fig. 2e). Moreover, the $\delta^{34}\text{S}$ value in leaf tissue was almost twice as low in the saline conditions

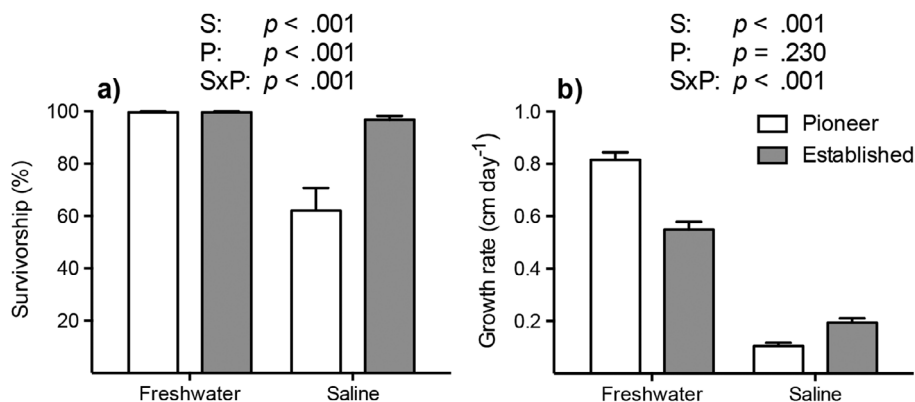


Fig. 1. Response of the individual shoots in both *Phragmites* treatments (pioneer vs. established) to fresh- and saltwater conditions. (a) Percentage of alive shoots after 39 d and (b) the growth rate of the shoots. S, P, and S \times P represent main effects of salinity (S), *Phragmites* treatment (P), and their interactions, respectively. Error bars represent +SE.

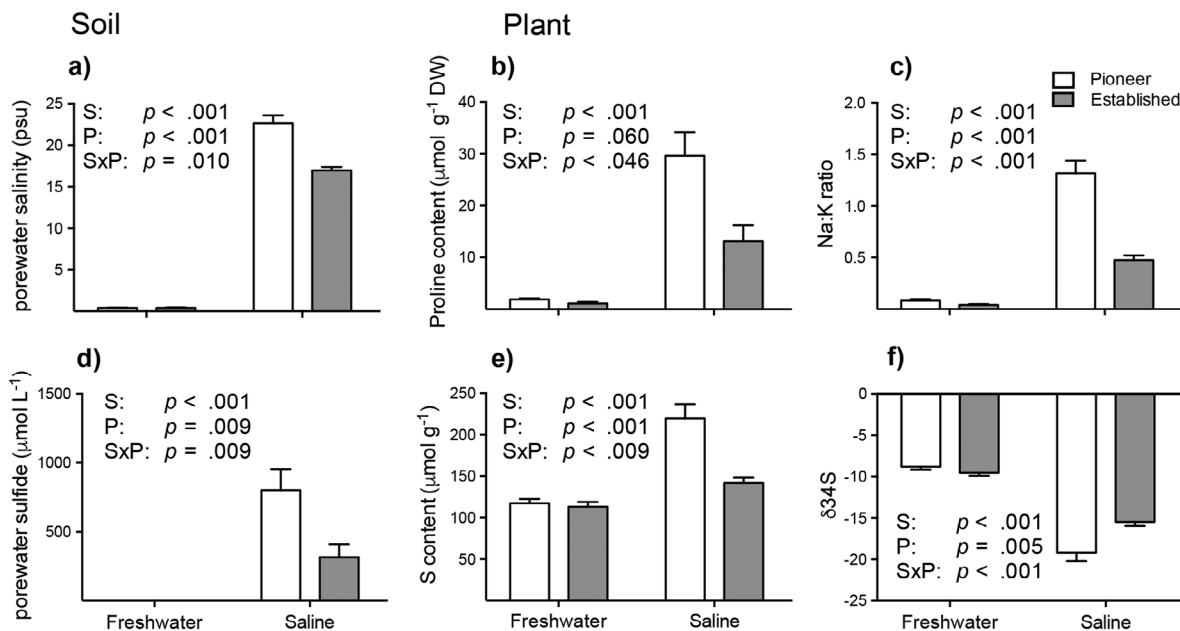


Fig. 2. Facilitative effects of *Phragmites australis* on both (a) porewater salinity and (d) porewater sulfide levels. Intraspecific facilitation led to decreased salinity levels which mitigated osmotic stress as measured by (b) proline levels and (c) Na:K ratio. Decreased sulfide levels led to (e) a lower total sulfur content of the shoots and (f) a lower $\delta^{34}\text{S}$, indicating lower sulfide uptake. S, P, and S \times P represent main effects of salinity (S), *Phragmites* treatment (P), and their interactions, respectively. Error bars represent +SE.

(-17.3 [S] vs. -9.2 [F]; $F_{1,47} = 341.4$; $P < 0.001$; Fig. 2f), reflecting higher sulfide uptake, and it was almost 20% higher in the pioneer versus the established community (-19.2 [PS] vs. -15.5 [ES]; $F_{1,47} = 24.0$; $P < 0.001$).

DISCUSSION

Despite the growing body of literature emphasizing the importance of intraspecific facilitation for the functioning and stability of many natural

ecosystems (Halpern et al. 2007, Silliman et al. 2015), its significance for explaining the persistence of unfavorable plant communities such as invasive species or weeds remains largely unexplored (Proença et al. 2019). Here, we experimentally demonstrate that, for *Phragmites australis*, density-dependent biogeochemical feedbacks strongly mitigate the negative effects of seawater flooding and therefore enhance its potential to persist in saline environments (see Fig. 3 for a graphical representation of these feedback mechanisms). In our experiment, we observed a clear shift from density-dependent competition in benign conditions to self-facilitation under environmental stress. In the freshwater treatment, we found the pioneer stands to have a higher growth rate compared to their established counterparts. Although seawater flooding negatively affected both the survival and growth of *Phragmites*, we found these negative effects to be strongly reduced in established *Phragmites* stands. Our findings show that in modified coastal ecosystems, shifts in habitat-forming species can be hard to reverse when intraspecific facilitation allows the newly established community to persist under a wide range of environmental conditions. We therefore urge the need to identify the underlying feedback mechanisms to design appropriate restoration efforts when restoration to a pre-disturbed state is desired.

Environmental conditions in salt marshes are detrimental to a wide range of species, as inundation by seawater leads to high soil salinity and anoxia. Both elevated salinity and anoxia-related high sulfide levels (generated by high rates of microbial sulfate reduction) are known to stunt the growth of *Phragmites* (Chambers et al. 2003). Whereas the majority of the plants in our pioneer treatment died or visibly suffered under saline conditions by losing photosynthetic tissue (Fig. 1; Appendix S1: Fig. S4), plants in our established treatment kept these two stressors at innocuous levels. Nutrient levels could not explain the observed effects (Appendix S1: Fig. S5), but we identified two plausible facilitative mechanisms for the observed stress alleviation: (1) a higher rainwater infiltration rate in the top layer of the intact *Phragmites* sods, leading to a dilution of the dissolved salt levels in the root mat, and (2) enhanced soil oxygenation

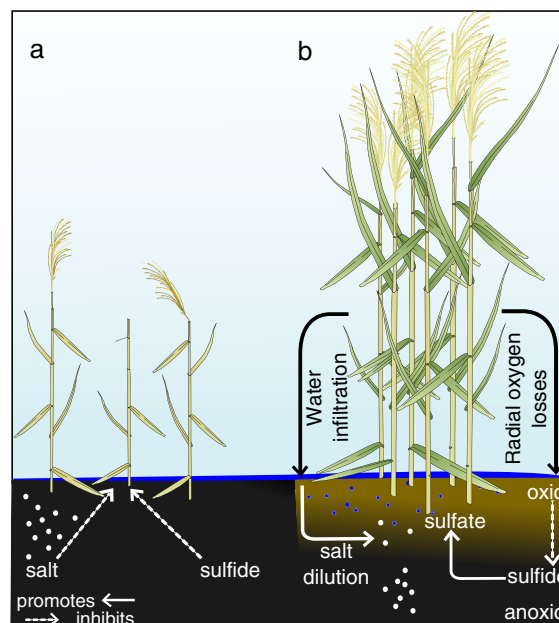


Fig. 3. Graphical representation of the positive feedback mechanisms that increase the persistence of established *Phragmites* communities in coastal wetlands that are subjected to seawater flooding. In the pioneer community (a), the harsh edaphic conditions (i.e., high salinity and sulfide levels) inhibit the growth of *Phragmites*. In the established community (b), however, *Phragmites* is able to overcome the detrimental edaphic conditions by (I) oxidizing the high soil sulfide levels by releasing oxygen from its roots and (II) diluting the high salinity levels by increasing the rainwater infiltration rate. Some of the symbols used in this figure were provided and modified with the courtesy of Tracey Saxby, IAN Image Library (ian.umces.edu/imagelibrary).

preventing the accumulation of phytotoxic sulfide (Fig. 2). Furthermore, measurements on the physiological responses of the plants confirmed that these were the most likely stress-alleviating feedback mechanisms. We found the plants in the established treatment to be able to overcome ionic stress and sulfide toxicity, respectively, by: (1) osmotic adjustment, preventing the uptake of excess sodium, and (2) a decrease in total sulfur content and, moreover, a lower fraction derived from sulfide intrusion (Fig. 2).

Similar to what we observed in our experiment, a positive feedback resulting from high rainwater infiltration and low evaporation in

dense vegetation stands compared to sparsely vegetated or bare soils is a well-known, ecosystem-structuring phenomenon in many arid and salt marsh ecosystems (HilleRisLambers et al. 2001, Qi et al. 2018). The extensive rhizome and root systems of the plant likely created a more open soil structure, increasing the soil's water-holding capacity and stimulating soil infiltration. In addition, shading from the much higher plant density may have also reduced evaporation. At the start of our experiment, salinity levels in our pioneer and established treatments were similar (19.4 ± 3.5 and 20.3 ± 2.7 psu for the pioneer and established treatments, respectively). However, in the pioneer treatments we witnessed a 15% increase in porewater salinity at the end of the experiment, whereas the salinity levels in the established treatments decreased by 15% (Fig. 2a). Elevated salinity levels increase the osmotic pressure of the porewater, which in turn impairs the water and nutrient uptake of plant species and may subsequently lead to ionic imbalances or even toxicity (Hartzendorf and Rolletschek 2001). We measured both the foliar free proline levels and the K^+ and Na^+ concentrations as a proxy for both osmotic adjustment and induced ionic toxicity and found large differences between the two *Phragmites* treatments in the saline conditions. Although the plants in the pioneer treatment accumulated twice as much proline, their $Na^+:K^+$ ratio was substantially higher due to both a lower contribution of K^+ and a twofold increase in Na^+ , indicating high salinity stress in these treatments. In contrast, both proline concentrations and $Na^+:K^+$ ratios in the plant tissue were much lower in established treatments, suggesting that habitat modification by increasing infiltration and decreasing evaporation rates can play an important role in escaping salinity stress.

In saline coastal ecosystems, sediment organic matter is decomposed by bacteria and archaea that use the abundant sulfate from seawater as an alternative electron acceptor instead of oxygen and produce toxic sulfide as a metabolic end product (Lamers et al. 2013). Radial oxygen losses (ROL) from the roots of many marine plants, such as cordgrass and seagrass, chemically oxidize sulfide in the rhizosphere, thereby preventing the detrimental effects of sulfide intrusion (Lee 2003, Calleja et al. 2007, van der

Heide et al. 2012). The observed threefold reduction of sulfide in the established *Phragmites* treatment (below the value of $400 \mu\text{mol/L}$ known to be toxic to *Phragmites*; Chambers 1997) compared to the pioneer treatment in saline conditions can be explained by density-dependent oxidation of the sediment (Howes et al. 1986, van der Heide et al. 2010; Fig. 2d). This experimental finding links to previous field studies on sulfide-mediated die-backs of *Phragmites* marshes in Europe (Armstrong et al. 1996, Armstrong and Armstrong 2001). The authors reported a remarkably clumped configuration of surviving plants in these degraded marshes. Dense *Phragmites* clumps were sometimes still vigorous and their persistence was speculated to be the result of locally enhanced sediment oxygenation, preventing the patches from succumbing, while high sulfide levels outside the patches limited lateral expansion. Our experimental results support this hypothesis as we detected a strong decrease in sulfide concentration within the established *Phragmites* treatments compared to their pioneer counterparts. Moreover, plants in the pioneer treatment showed a clear physiological response to sulfide exposure as indicated by blackened root tips, enhanced sulfur concentration in the leaf tissue, and a lower $\delta^{34}\text{S}$ value (Fig. 2e, f), which indicates enhanced sulfide intrusion (Carlson and Forrest 1982, Holmer and Hasler-Sheetal 2014). Overall, we conclude that dense *Phragmites* stands can overcome sulfide toxicity by joint detoxification through radial oxygen loss.

We identified two distinct density-dependent self-reinforcing mechanisms—sulfide detoxification and alleviation of salinity stress—that are likely to act in concert or even synergistically to increase *Phragmites* persistence in (restored) saline coastal marshes. Although many habitat-modifying species generate multiple feedbacks, the potential importance of interactions between feedbacks on ecosystem dynamics has only recently been addressed by two studies (van de Leemput et al. 2016, Maxwell et al. 2017). For coastal and inland marshes dominated by *Phragmites*, salinity stress may lead to sulfide accumulation, because *Phragmites* plants that suffer from ionic stress often exhibit stunted growth, which in turn likely reduces radial oxygen losses to the rhizosphere (Rolletschek and Hartzendorf 2000). Furthermore, both sulfide toxicity and ionic stress

can lead to impaired nutrient (N, P) uptake, which may restrict plant growth (Lamers et al. 2013). In addition, *Phragmites* shows high genetic variability between geographic regions, which could potentially impact the strength of the observed intraspecific facilitative mechanisms (Hansen et al. 2007). Overall, we conclude that the outcome of facilitative mechanisms is likely context-dependent and may therefore differ across contrasting environments and genotypes. In our mesocosm experiment, for example, we found a surprisingly strong shift from self-facilitation to competition. Whereas facilitation was the dominant interaction type in the salinity treatment, competition became the main driver in freshwater conditions, as indicated by a slower growth response in the established treatment compared to the pioneer treatment. This finding is in line with the stress-gradient hypothesis, which predicts a shift from competition to facilitation with increasing physical stress levels (Bertness and Callaway 1994, He et al. 2013). In our mesocosm experiment, we tested only two salinity levels (~0 vs. 20 psu), while in natural conditions, salinity increases along a gradient over which plant interactions gradually shift from competition to facilitation with increasing salinity. Facilitation finally collapses at salinity levels exceeding the physiological tolerance of *Phragmites australis* (Michalet et al. 2006, Qi et al. 2018; Appendix S1: Fig. S1). So far, most experiments on the stress-gradient hypothesis have been performed in the field and focused on interspecific facilitation enhancing biodiversity and productivity in plant communities (Bertness and Callaway 1994, Maestre et al. 2009). Recently, however, the effects of intraspecific or self-facilitation are more explicitly acknowledged (Fajardo and McIntire 2011, Qi et al. 2018, Proença et al. 2019). Our experimental setup allowed us to study the effects of intraspecific facilitation without potential interactions with other species enabling us to identify two positive feedback mechanisms that can increase the persistence of a relatively salt-intolerant species in saline field conditions.

Our study emphasizes that intraspecific facilitation may act as a double-edged sword in restoration ecology, by increasing the resilience of management target species but also complicating the eradication or restoration of nontarget communities. Recently, it was shown that harnessing

positive intraspecific interactions in restoration designs—by clumping rather than spacing out individuals—can greatly enhance restoration successes of lost habitat-forming species in degraded systems (Silliman et al. 2015, Harpenslager et al. 2016, de Paoli et al. 2017, Derksen-Hooijberg et al. 2018). Our study underlines these previous findings, but also calls for an extension of this framework: Rather than harnessing positive interactions, efforts to restore target species in ecosystems dominated by unwanted habitat-modifying species should be aimed at breaking these self-facilitative feedback mechanisms. This requires a change in management perspective as current restoration practices are typically aimed at restoring pre-disturbance abiotic conditions to rehabilitate the original plant community and ecosystem functions (Zhao et al. 2016). This may, however, be insufficient for coastal ecosystems invaded or dominated by unwanted habitat-modifying species. In such cases, we argue that for successful restoration to pre-disturbed conditions, the first aim should be on breaking the intra- or interspecific facilitative interactions of the nontarget community. This can, for instance, be achieved by temporarily increasing the environmental stress beyond the species' buffering capacity or by actively removing biomass to initiate a collapse of facilitative bonds (see Appendix S1: Fig. S1 for a graphical representation; Michalet et al. 2006, Halpern et al. 2007). Successful removal of the nontarget community may then be followed up by restoring the original communities, while taking their possible dependence on facilitative interactions into account. Our study highlights the critical role of intraspecific facilitation in coastal wetlands. We therefore argue that active restoration measures such as sod-cutting, the removal of tidal restrictions, and extended periods of seawater intrusion are necessary to restore modified wetlands to pre-disturbed conditions and rehabilitate the original halophytic communities.

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DATA AVAILABILITY

Data available via the Data Archiving and Networked Services (DANS) EASY <https://doi.org/10.17026/dans-x35-pms2>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2842/full>